TRICHOTHYRIACEOUS FUNGI FROM THE EARLY TERTIARY OF SOUTHERN ENGLAND

by PETER H. SMITH

ABSTRACT. Isolated ascocarps (thyriothecia) from Upper Eocene deposits of the Hampshire Basin are described as a new species of the genus *Trichothyrites* Rosendahl within the Trichothyriaceae, a family of epiphyllous fungi not previously recorded from English Tertiary deposits. Comparisons are made between the fossil material and the extant genus *Trichothyrina* Petrak to establish their affinity. Earlier records of epiphyllous fossil fungi from British deposits are reconsidered in view of recent taxonomic changes in living taxa.

IN the course of an examination of fungal material from the Leaf Bed (Bed X of Tawney and Keeping 1883), of the Lower Headon deposits (Upper Eocene/Lower Oligocene) from Hordle Cliff, Hampshire, thyriothecia ascribable to the Trichothyriaceae have been recognized (see Smith 1978 for grid reference and methods of isolation). Examples of this type of fructification have not previously been described from deposits earlier than Quaternary in Britain.

Although ascomycetous fungi have been shown to be present in fossil deposits of Upper Carboniferous age (Batra *et al.* 1964) it is interesting to note that the majority of fossil epiphyllous ascomycete forms are reported only from Tertiary deposits. As shown by Tiffney and Barghoorn (1974) the bulk of Tertiary ascomycetes are epiphyllous forms occurring in association with leaf cuticles. Graham (1962) attributes this to rapid adaptive radiation of the ascomycetes to capitalize on the vast expansion of potential habitats within the phyllosphere following the appearance of the angiosperms. However, as Tiffney and Barghoorn caution, this apparent rapid diversification and numerical increase in fossil forms may in part be due to the large number of palaeobotanical investigations made upon leaf bed deposits from the Tertiary. Apart from the epiphyllous fungi from the Lower Cretaceous flora described by Krassilov (1967), there is little published evidence to suggest that a diverse epiphyllous fungal flora existed prior to the Tertiary. This could well be due to the fungal element being overlooked or disregarded as not worthy of further investigation by workers concentrating on the leaves themselves.

The presence of fructifications of epiphyllous fungi in Tertiary fossil deposits has generally been accepted as indicating warm sub-tropical to tropical climatic conditions, in light of the predominantly tropical distribution of extant taxa of the Microthyriales. This contention is reinforced by the comparative work on fossil and extant forms of epiphyllous fungi of Lange (1976, 1978) from the Southern Hemisphere.

TAXONOMIC CONSIDERATIONS

Considerable recent advances have been made in the understanding of the taxonomic relationships of extant taxa (Müller and von Arx 1962; Luttrell 1973). Few workers interested in fossil forms have had these modern treatments available for consultation, and have often tended to use 'microthyriaceous' in an all-embracing term. Records of British fossil epiphyllous fungi can now be ordered as follows (see Table 1) using the classification of Luttrell (1973). Godwin and Andrew (1951) reported the common occurrence of *Microthyrium*-like thyriothecia (with a tentative affinity with *Loranthomyces* von Höhnel of the Trichothyriaceae) in Post-Glacial peat deposits ranging from the Pennines to Somerset. Vishnu-Mittre (1973) attributed thyriothecia from Flandrian peat deposits at Whittlesey Mere to two extant species, *M. culmigenum* Sydow and *M. nigro-annulatum*

[Palaeontology, Vol. 23, Part 1, 1980, pp. 205–212.]

TABLE 1

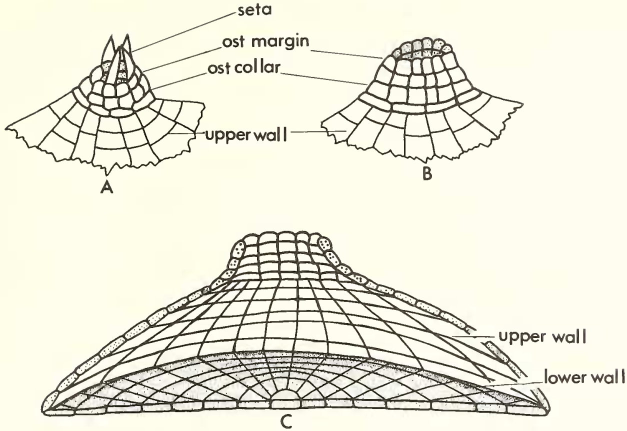
CLASS LOCULOASCOMYCETES

ORDER: MICROTHYRIALES	ORDER: DOTHIDEALES
FAMILY: MICROTHYRIACEAE	FAMILY: TRICHOTHYRIACEAE
	Microthyrium-like cf. *Loranthomyces* von Höhnel, 1917 (Godwin and Andrew 1951)
Microthyrium culmigenum Sydow, 1921 → (From Vishnu-Mittre 1973)	*Trichothyrina alpestris* (Sacc.) Petrak, 1950 (From Ellis 1977)
Microthyrium nigro-annulatum Webster, 1952 → (From Vishnu-Mittre 1973)	*Trichothyrina nigro-annulata* (Webst.) Ellis, 1977 (From Ellis 1977)
*Phragmothyrites** *eocenica* Edwards, 1927	
*Phragmothyrites** *hibernica* Johnson, 1949	
FAMILY: MICROPELTIDACEAE	
*Stomiopeltites** *cretacea* Alvin and Muir, 1970	

* Denotes fossil genus.

Webster, and commented upon the similarity of the material to that described by Godwin and Andrew. Ellis (1977), however, in her critical taxonomic review of extant British Microthyriaceae, has removed the species cited by Vishnu-Mittre both from the genus *Microthyrium* and the family Microthyriaceae (see Table 1). Based largely upon differences in thyriothecial construction, both species have been placed in the genus *Trichothyrina* Petrak in the family Trichothyriaceae. These are the only Dothidealian fungi in the fossil record from Britain. Microthyrialian fungi are only slightly better documented. Alvin and Muir (1970) erected the genus *Stomiopeltites* for fructifications resembling those of *Stomiopeltis* Theissen from the family Micropeltidaceae. These fossil forms were borne on leafy conifer shoots from the Lower Cretaceous deposits of the English Wealden. Edwards (1922) described *Phragmothrites eocenica* based on fructifications borne on conifer leaves of Eocene age from Mull, Scotland, whilst Johnson (1949) described *P. hibernica* on cuticles attributed to *Fagus* from an Eocene deposit of Ireland.

Selkirk (1975) has enumerated the difficulties involved in positive identification of thyriothecia from fossil deposits as members of the Trichothyriaceae, rather than Microthyriaceae the uncertainties involved being centred upon details of thyriothecial construction. These concern the ostiole borne on a short papilla of thickened cells often, but not always, bearing setae on the uppermost ring of ostiolar collar cells (see text-fig. 1A and B), and the cellular pattern and construction of the thyriothecium. In contrast to the dimidiate construction of fructifications of Microthyriaceae where the lower wall is extremely thin and delicate, those of Trichothyriaceae are complete with well-developed upper and lower walls, each composed of radiate files of cells which appear almost isodiametric in surface view (see text-fig. 1C). This pattern of cellular arrangement of quadrilateral cells is also present in the upper wall of the thyriothecia of Microthyriaceae close to the ostiole, but cells generally become more elongate towards the margins.



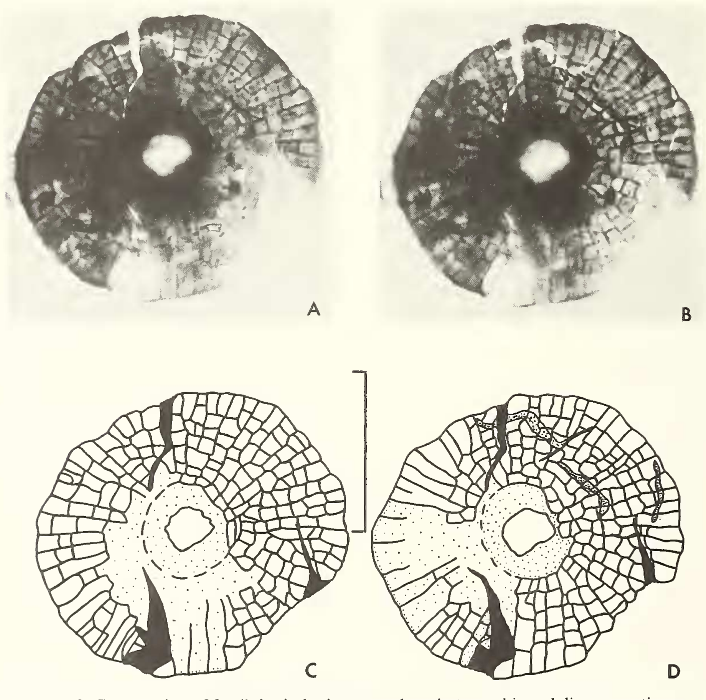
TEXT-FIG. 1. Diagrammatic representations of thyriothecium constructions in Trichothyriaceae. A, ostiole bearing setae on ostiolar margin. B, ostiole with smooth ostiolar margin. C, vertical section of the thyriothecium showing 3D structure. ost = ostiolar.

Microscopic examination of the Hordle Cliff thyriothecia has resulted in the recognition of several criteria that it is felt allow accurate assignment of the fructifications as those of Trichothyriaceae. The papilla bearing the ostiole has retained sufficient height in the fossils to remain a distinguishing feature. Despite dorsiventral compression of the entire fructification the thickened cells of the papilla usually remain erect and thus the terminal ostiole is observable in a higher focal plane than the cells of the upper wall of the fructification. Compression of the fructification and subsequent preparation treatment often leads to rupture of the walls enabling the presence of a well-defined and complete lower wall to be seen (seen text-fig. 2).

Rosendahl (1943) used the features of a complete fossil thyriothecium (i.e. possessing both upper and lower walls), with an erect ostiolar collar and the marginal cells of the pore bearing setae, to describe *Trichothyrites pleistocaenica*. This species was found in association with both spruce needles and moss leaves from an early Pleistocene deposit from Minnesota. Those found on spruce needles were reported to be in close association with other fungal hyphae which were tentatively identified as a species of *Herpotrichia*. The relationship between these hyphae and the thyriothecia, however, remained problematic; no definite myco-parasitic relationship could be demonstrated. Myco-parasitism was further questioned on the grounds of the presence of apparently identical fructifications on moss leaves where no other fungal hyphae were demonstrable. Rosendahl therefore concluded that *T. pleistocaenica* was saprophytic, but no comparison was made with extant species. Since publication of Rosendahl's description, however, Petrak (1950) has elevated from subgeneric to generic level the taxon *Trichothyrina* for predominantly saprophytic fungi, as opposed to *Trichothyrium* Sacc. which is characterized as being a genus parasitizing other fungi. This would suggest that the closest affinity for *Trichothyrites* Rosendahl, would be this extant genus *Trichothyrina* Petrak. This is further borne out by an examination of the Hordle Cliff material. Here the thyriothecia are not associated with host material in most instances, but those that have been observed attached to cuticle are not in association with any other fungal hyphae, which would appear to preclude any suggested myco-parasitic relationship.

Size measurements used by Ellis (1977) in defining living species of *Trichothyrina*, would also suggest close affinity of the Hordle Cliff material with extant species. However, one of the major diagnostic features for separation of living species remains their mode of nutrition, a character impossible to ascertain with certainty in fossil material.

A number of fructifications of epiphyllous fungi from the Tertiary of the Southern Hemisphere and Lower Cretaceous of Siberia have been assigned to the genus *Notothyrites* (Cookson 1947; Selkirk 1975; Kemp 1978; Krassilov 1967). This genus bears a close resemblance to the material described here with the exceptions that no mention of a lower thyriothecial wall has been made in the descriptions nor shown in any of the specimens that have been figured. On these grounds *Notothyrites* has hitherto been considered as a genus of the Microthyriaceae. As no detailed comparison with the Southern Hemisphere material has yet been made it seems appropriate, at present, to retain *Trichothyrites* Rosendahl with an emended diagnosis allowing the incorporation of the Hordle Cliff material.



TEXT-FIG. 2. Construction of fossil thyriothecium. A and C, photographic and diagrammatic representation of upper thyriothecial wall. B and D, the same specimen at a lower depth of focus showing splits in upper wall and presence of lower wall. Scale bar = 50 μm.

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Genus TRICHOTHYRITES Rosendahl, 1943 emend.

Emended diagnosis. Thyriothecia appearing disc or saucer-shaped due to compression; possessing definite upper and lower walls of radiate rows of almost square cells (3–8 μm × 3–8 μm). Cell walls of upper layer of thyriothecium generally more strongly thickened than those of the lower layer. Thyriothecia ranging from 70 μm to 200 μm in diameter and bearing on upper wall an erect ostiolar collar (papilla) made up of from two to six tiers of small (2 μm × 2 μm) extremely thick-walled quadilateral cells. Uppermost tier (ostiolar margin) of cells may have short prolongations (setae) in some cases. Thyriothecial outline usually smooth but may appear lobate.

Type species. Trichothyrites pleistocaenica Rosendahl (1943), figs. 8–10, p. 132; figs. 18–20, p. 135.

Trichothyrites hordlensis sp. nov.

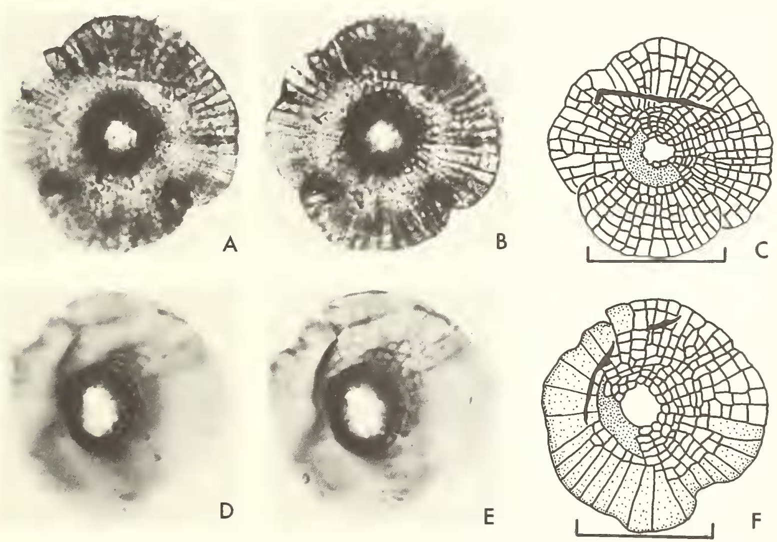
Text-fig. 3A–F

Holotype. Text-fig. 3A, B, and C, British Museum (Natural History), Department of Palaeontology slide no. V60215.

Type locality. Hordle Cliff, Hampshire (Grid ref. SZ262923).

Horizon. Hordle Leaf Bed (Upper Eocene/Lower Oligocene).

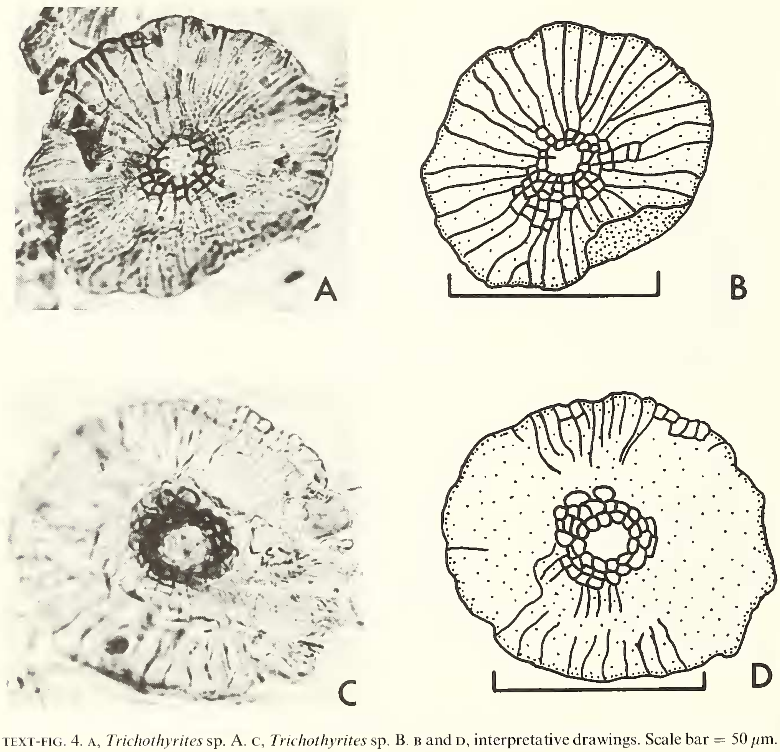
Diagnosis. Maximum diameter of thyriothecia 75 μm. Erect ostiolar collar of 3–4 tiers of small (2 μm × 2 μm) thick-walled quadrilateral cells, diameter of collar 20 μm; ostiolar marginal cells not produced into setae,



TEXT-FIG. 3. *Trichothyrites hordlensis.* A and B, fructifications at two focal planes showing thyriothecial construction especially upper wall. D and E, details of ostiolar region of *T. hordlensis.* C and F, interpretative drawings of specimens. Scale bar = 50 μm.

ostiolar pore diameter 10–15 μm. Upper wall of thyriothecium consisting of quadilateral cells arranged in rows radiating from ostiolar collar, cell size ranging from 3 μm × 3 μm near collar to 6 μm × 8 μm at margin. Cells of lower wall similar but with more delicate cell walls. Thyriothecia usually found as isolated structures not in association with cuticle or other fungal hyphae. Spores absent.

Discussion. The affinity of these fossil thyriothecia cannot be stated exactly as the final diagnostic character used for species determination by Ellis (1977) is the nature of the host substrate coupled with the shape of the ascopores. Although the large cells at the base of the ostiolar collar (see text-fig. 3A, B) may tend to suggest an affinity with *Trichothyrina alpestris* (Sacc.) Petrak, 1950, there is no clear indication that these cells are perforate in the fossil material. Similarly, although setal processes from the cells of the ostiolar may or may not be present in *T. alpestris*, their absence from the fossil material, coupled with the small over-all size of the fructification (75 μm v. 200 μm), small ostiolar collar diameter (20 μm v. 25–40 μm), all combine to suggest a closer affinity with *T. ammophilae* Ellis, 1977.



TEXT-FIG. 4. A, *Trichothyrites* sp. A. C, *Trichothyrites* sp. B. B and D, interpretative drawings. Scale bar = 50 μm.

Trichothyrites sp. A

Text-fig. 4A, B

Fructifications of this type are present in the Hordle Cliff material at a much lower frequency than those of *Trichothyrites hordlensis*. Insufficient numbers have been isolated so far to erect a detailed specific diagnosis but a tentative affinity with *Trichothyrina pinophylla* (von Hohn.) Petrak, 1950 is suggested due to the smaller number of tiers in the ostiolar collar and the much smaller (60 μm) overall diameter of the fructification.

Trichothyrites sp. B

Text-fig. 4C, D

Again, insufficient material precludes a formal specific diagnosis for this type of fructification; however, the characteristic appearance of the ostiolar collar due to the outward curvature of the cells of the ostiolar margin allows easy separation from the two preceding forms. Affinity with *Trichothyrina nigro-annulata* (Webster) Ellis, 1977 is suggested.

CONCLUSIONS

Previous records have concentrated upon Microthyriaceous forms within the Tertiary. The demonstration of Trichothyriaceous forms from the Upper Eocene is indicative that these fungi also were involved in the apparently rapid diversification of ascomycete groups during the Tertiary. Careful re-examination of material from pre-Tertiary deposits to establish the presence or absence of epiphyllous fungi, similar to the Trichothyriaceae would be of great interest. This might establish whether, with the advent of the angiosperms, the Trichothyriaceae arose as epiphyllous forms and only later attained their present far more specialized myco-parasitic nature.

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Typescript received 30 September 1978

Revised typescript received 28 January 1979